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Factors Influencing Year-Class Strength of Percids: A Summary and a Model of Temperature Effects¹

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Factors regulating year-class strength in the percid genera *Stizostedion* and *Perca* are summarized. Some index of water temperature regime correlates significantly with year-class strength of percids in many water bodies. Moderate synchrony of year-class strength is noted for walleye (*Stizostedion vitreum vitreum*) in several lakes in North America. A probabilistic model is proposed to explain the basis of temperature dependence of year-class strength in percids, but tests of the model using Lake Erie data indicated that observed correlations between temperature and year-class strength of yellow perch (*Perca flavescens*) and walleye may not be the result of direct effects of the temperature regime on survivorship of early life-history phases.

Key words: Percidae, year-class strength, temperature, probabilistic model, early life history

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Nous résumons les facteurs contrôlant l'abondance des classes d'âge des genres de percidés *Stizostedion* et *Perca*. Dans plusieurs plans d'eau, il y a corrélation significative entre un indice du régime des températures de l'eau et l'abondance des classes d'âge de percidés. On note une synchronie modérée dans l'abondance des classes d'âge du doré jaune (*Stizostedion vitreum vitreum*) dans plusieurs lacs nord-américains. Nous proposons un modèle probabiliste pour expliquer comment l'abondance des classes d'âge des percidés dépend de la température. Mais des essais du modèle avec des données du lac Érié indiquent que les corrélations observées entre la température et l'abondance des classes d'âge tant de perchaudes (*Perca flavescens*) que de dorés jaunes peuvent ne pas être le résultat d'effets directs du régime de températures sur la survie au début du cycle biologique.

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In this paper we summarize the major factors thought to regulate year-class strength in the

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genera *Stizostedion* and *Perca*. We also report a tentative pattern of year-class synchrony in North America and advance a model based on the temperature dependence of mortality in early life history to explain variation in the year-class strength of species in these two genera. Contributions to the PERCIS Symposium revealed the universality of fluctuations in year-class strength in populations of species in the two

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genera. The phenomenon was mentioned in at least 23 of the papers presented, which represented water bodies varying in area, depth, flushing rate, intensity of exploitation, and the species composition of associated fishes. For the Eurasian species, the range of the fluctuation was greater for Eurasian perch (*Perca fluviatilis*) than for pikeperch (*Stizostedion lucioperca*). In Lake IJssel, for example, Willemsen (1977) reported that the ratio of the strongest to weakest year-class was 100 for perch and 20 for pikeperch. Kipling (1976) reported a large (400-fold) variation in perch year-class strength in Lake Windermere and year-class strength fluctuations of pikeperch have been observed to range from 10-fold to 55-fold in other European water bodies (Boiko 1964; Lind 1977; and Rundberg 1977). In North America, yellow perch (*Perca flavescens*) and walleye (*Stizostedion vitreum*) have similar patterns of fluctuation of year-class strength. Yellow perch year-class strength has been reported to vary from 8-fold to 40-fold (Forney 1976; Smith 1977; Eshenroder 1977; Nelson and Walburg 1977). Walleye, in comparison, is reported to have year-class strength fluctuations of 12-fold-74-fold (Spangler et al. 1977; Smith 1977; Forney 1976; Carlander 1977; Kempinger and Carline 1977; Nelson and Walburg 1977; Busch et al. 1975). In some lakes yellow perch seem to have a greater variation in year-class strength than walleye (Forney 1976; Smith 1977), but the pattern is reversed elsewhere (Leach and Nepszy 1976).

Attempts to analyze the patterns of fluctuation ultimately are limited by the variation in methods of estimating year-class strength. Methods used include year-class contribution to a fishery, catch per unit effort for reference gears, mark-and-recapture technique, and trawl catches of year 0 juveniles. Not all of these methods yield the same estimates of year-class strength (e.g. Forney 1976). Thus, the comparison between water bodies of the amplitude of fluctuation in year-class strength of any species is limited. Nevertheless, the year-class strength of these fishes appears to be fixed either by the year 0 juvenile stage (Busch 1975; Willemsen 1977) or by midsummer of the 2nd yr, year 1 juveniles (Forney 1976).

Factors Associated with Year-Class Strength

Various factors have been associated with the determination of year-class strength in percids. The most important physical factors appear to be water temperature, wind, and water level of rivers or flow rate of rivers. Less often, reports mention water transparency, oxygen concentration, and salinity of spawning grounds. Biotic factors

include predation, cannibalism, prey availability, and size of spawning stock or stocking intensity. Although all of these factors may be interrelated, the water temperature regime may affect mortality rates directly or indirectly through any of the other factors and may thus be an ultimate cause of variation in year-class strength for many water bodies.

Most studies we reviewed implicated water temperature as a dominant factor regulating year-class strength. Using a variety of measures of the temperature regime, many authors found a positive correlation between water temperatures and survivorship of one or more development phases. Busch et al. (1975) found strong correlations between rates of spring warming and both total egg production and fry densities for a 10-yr period in Lake Erie. Eshenroder (1977) reported a similar relationship for yellow perch in Saginaw Bay for a 24-yr period. Nagięc (1977) reported the highest correlation between mean monthly temperature during spawning and incubation and the abundance of pikeperch year-classes. Positive correlations between air temperature and year-class strength were also reported (Svardson and Mölin 1973), but other attempts to find correlations with air temperature have not produced significant relationships (Doan 1942; Jobes 1952; El-Zarka 1959; Heyerdahl and Smith 1971).

Apart from these attempts to find correlations, some studies showed the climatic regime to act on year-class strength in a discontinuous manner. Periods of cold weather, for example, seem to be associated with weak year-classes (Derback 1947; Smith and Krefting 1953; Walburg 1972). Bagenal (1977) and Kipling (1976) showed that weak year-classes of perch in Lake Windermere are always associated with cold summers (<150 degree-days above 14°C). Other authors noted that warm summers seem to produce strong year-classes (Payne 1964; Kuznetsov 1970). Only three studies in the PERCIS Symposium indicated lack of any relationship with water temperature (Carlander and Payne 1977; Kempinger and Carline 1977; Willemsen 1977).

The importance of the other physical factors (wind, water level, and flow rate) appeared to be less general. Mean daily wind velocity accounts for much of the variation in survival of early stages of yellow perch in Oneida Lake (Clady 1976), but in other studies wind does not correlate significantly with strength of year-class (Busch et al. 1975). For river spawning populations of walleye, Spangler et al. (1977) reported a positive relationship between flow rate and strength of year-class. A positive association between water level and year-class strength in walleye and pikeperch has also been reported for

Class Strengths

the PERCIS to find a pattern of in to various lakes. rance of water tem- climatic effects might in certain geograph- iduals to determine year-classes of any l in the water bodies We obtained these European lakes and ge lakes in North American lakes, we rony. At least 20% 1 strong year-classes 62, 1965, and 1972. rony is noteworthy, we acquired needs prospect, we should -class timing. Never- uggest some under- noted by Eshenroder ped more rigorously

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r-class strength may anage to a sequence g. To use this ed direct effects rvivorship of early erch. Other factors redation, and can- perature dependent, robabilities, but in- ate their regulatory ollowing discussion data used to con- cepts in Fig. 1.

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TABLE 1. Years during 1940-76 in which strong year-classes of percids* were reported in the PERCIS Symposium for various European and North American Lakes. Within each group, lakes are listed in order of increasing latitude.

Lake	Year									
	1	2	3	4	5	6	7	8	9	0
<i>European lakes</i>										
Baalton										
Constance										
Klivaca										
IJssel										
Jesiorak										
Windermere										
Loch Leven										
Hjälmaren										
Mälaren										
Kolliolampi										
<i>North American lakes</i>										
Norris Res.										
Erie										
St. Clair										
Clear Lake										
Bay of Quinte										
Oneida										
Huron										
Georgian Bay										
Winnebago										
Pike Lake										
Green Bay										
Oahe										
Escanaba										
Mille Lacs										
Leech										
Red Lakes										
Lake of the Woods										

*X, *Perca fluviatilis*; 0, *Stizostedion leucioerca*; W, *Stizostedion vitreum vitreum*.

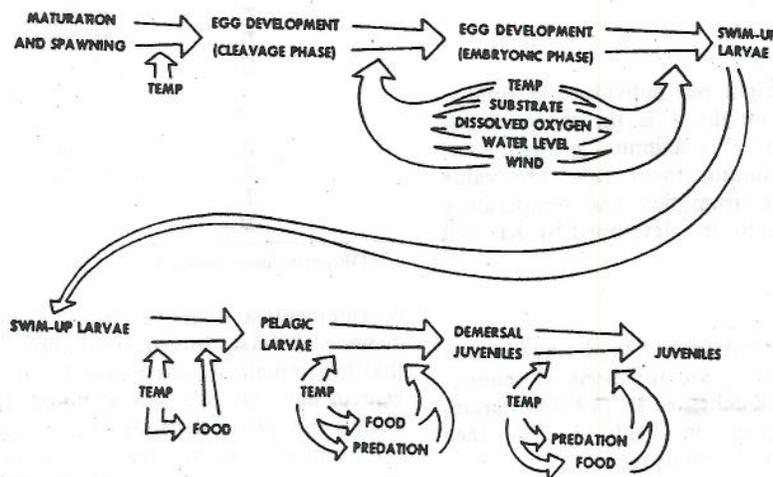


FIG. 1. Interactions of factors that determine year-class strength of *Perca* and *Stizostedion* species.

affects survival (Hokanson and Kleiner 1974). Using these two relationships, we relate the probability of survival through this stage by

$$(1) P_1 = 1 - \sum_{i=1}^n {}^1D_i$$

where n is the number of days required to complete the phase and 1D_i is the temperature-dependent death rate calculated from Hokanson (1977). Because the time required to complete the phase is temperature dependent, we had to assume a daily rate of development, which is also temperature dependent. On a rising temperature regime, we considered the phase completed when the cumulative development equals or exceeds a value of 1.0. Temperature dependence of mortality rate is given in Table 2, and development rates at various temperatures are

Temp (°C)	Development rate (day ⁻¹)	
	Cleavage egg	Embryo
3	0.071	0.028
6	0.154	0.028
9	0.283	0.043
12	0.444	0.075
15	0.611	0.125
18	1	0.154
21	1	0.2
24	1	0.2
27	1	0.2
30	1	0.2

Probability of surviving the embryonic phase — We calculated survival of this phase in a manner similar to that for the cleavage-egg phase.

TABLE 2. Daily mortality rates for phases of yellow perch from cleavage egg to swim-up larvae

Temp (°C)	Cleavage egg	Embryo	Swim-up larvae
3	0.050	0.027	1.0
6	0.005	0.018	0.85
9	0.003	0.018	0.42
12	0.000	0.015	0.12
15	0.050	0.019	0.02
18	0.160	0.008	0.0
21	0.70	0.020	0.08
24	1.0	0.150	0.20
27	1.0	0.2	0.45
30	1.0	0.2	1.0

Again using the data of Hokanson and Kleiner (1974) we implement the following function:

$$(2) P_2 = 1 - \sum_{i=1}^n {}^2D_i$$

where n is the number of days required to complete the phase and 2D_i is the temperature-dependent death rate. Development rates and death rates were computed from Hokanson (1977) as described above. Values for development rates are summarized above and mortality rates are given in Table 2.

Probability of surviving swim-up phase — The swim-up phase corresponds to the eleutheroembryonic phase described by Balon (1975). We treated the temperature dependence of survival in the same way as for egg development. Hokanson (1977) reported that development times for this phase were approximately 1 day

and that survival was temperature dependent, thus defined survival probability as

$$(3) P_3 = 1 - {}^3D_i$$

where 3D_i is the daily death rate.

Probability of surviving the juvenile phase — We assumed that an individual survives the juvenile phase at some weight and phase until a minimum growth relationship is

$$(4) B_t = B_0 e^{k g_m t}$$

where B_t is the weight at time t , B_0 is the starting weight, k is a temperature-dependent fraction of maximum growth, and g_m is the maximum growth rate. The value of k depends on consumption in a manner similar to that of Hokanson et al. (1974, 1977):

$$(5) k = p r_c - r_R$$

where p is a coefficient of prey, and r_c and r_R are the growth rate and maintenance rate described by Kitchener (1974). Instantaneous values are given to estimate survival of the

$$(6) P_4 = e^{-\sum_{i=1}^n {}^4D_i}$$

where 4D_i is the temperature-dependent mortality rate and t_m is the time to reach minimum weight. The instantaneous mortality coefficients for various temperatures are given in Table 2 from McCormick (1977).

Temp (°C)

- 3
- 6
- 9
- 12
- 15
- 18
- 21
- 24
- 27
- 30

Unfortunately, these data were not obtained for juvenile survival. The data for the pelagic larvae to juveniles phase are not available. No data are available for the mortality parameters for the juvenile phase.

Probability of surviving the juvenile phase — Fish in this phase...

SWIM-UP LARVA

and that survival was temperature dependent. We thus defined survival probability for this phase as

$$(3) P_3 = 1 - {}^3D_t$$

where 3D_t is the daily death rate (Table 2).

Probability of surviving pelagic larvae phase — We assumed that an individual larva starts this phase at some weight and continues in the pelagic phase until a minimum weight is achieved. The growth relationship is

$$(4) B_t = B_0 e^{kz_m t}$$

where B_t is the weight per individual at time t , B_0 is the starting weight, k is the temperature-dependent fraction of maximum growth rate, and g_m is the maximum growth rate. The value of k depends on consumption and temperature in a manner similar to that developed by Kitchell et al. (1974, 1977):

$$(5) k = pr_c - r_R$$

where p is a coefficient related to the availability of prey, and r_c and r_R are functions of temperature described by Kitchell et al. (1977). Parameter values are given in Table 3. We then estimate survival of the phase by

$$(6) P_4 = e^{-\sum_{i=1}^m {}^4D_i}$$

where 4D_i is the temperature-dependent death rate and t_m is the time required to complete the phase. The instantaneous daily mortality coefficients for various temperatures were calculated from McCormick (1976):

Temp (°C)	Instantaneous mortality (day ⁻¹)
3	0.0002
6	0.0002
9	0.0010
12	0.0058
15	0.0050
18	0.0030
21	0.0030
24	0.0040
27	0.0004
30	0.0002

Unfortunately, these mortality coefficients were obtained for juvenile yellow perch. We suspect the pelagic larvae to be more stenothermic, but no data are available to obtain more suitable parameters for the model.

Probability of surviving demersal juvenile phase — Fish in this phase have completed larval

TABLE 3. Parameter values for larval growth in equations 4 and 5. Both r_c and r_R are temperature dependent functions described by Kitchell et al. (1977).

Parameter	Value
g_m	0.052 · day ⁻¹
B_0	1.0 mg/ind
B_m	150.0 mg/ind
p	1.0 ^a
<i>r_c constants</i>	
T_m	32.0°C
T_0	23.0°C
Q_{10}	2.3 ^a
<i>r_R constants</i>	
R_m	0.14 ^a
T_m	35.0°C
T_0	28.0°C
Q_{10}	2.1 ^a

^aDimensionless constant.

development and move from a pelagic to a demersal habitat. In our simulations we assumed that fish remain in this phase for the rest of the year to day 360. We also assumed that mortality during this phase depended on temperature, and the probability of survival was determined by

$$(7) P_5 = e^{-(\alpha t_m + \sum_{i=1}^m {}^5D_i)}$$

where 5D_i is the same temperature-dependent death rate used for the pelagic larvae and α is the base natural mortality, which we assumed to be 0.017 · day⁻¹.

The relative year-class strength, or joint-survival probability, was calculated

$$(8) P = P_1 \cdot P_2 \cdot P_3 \cdot P_4 \cdot P_5 \cdot 0.6$$

Actual year-class strength could be calculated from estimates of the density and fecundity of the brood stock. As a test of the model calibration, we compared (Fig. 2) the survival probabilities of the three early development phases of yellow perch with the experimental data of Hokanson and Kleiner (1974). The good agreement then allowed us to test the model on a variable temperature case.

Application of Model to Perch and Walleye in Lake Erie

We chose to test the model by comparing observed and predicted year-class strengths of perch and walleye in Lake Erie. Three factors

erca
or phases of yellow perch
vae

Embryo	Swim-up larvae
0.027	1.0
0.018	0.85
0.018	0.42
0.015	0.12
0.019	0.02
0.008	0.0
0	0.08
0	0.20
0	0.45
0.2	1.0

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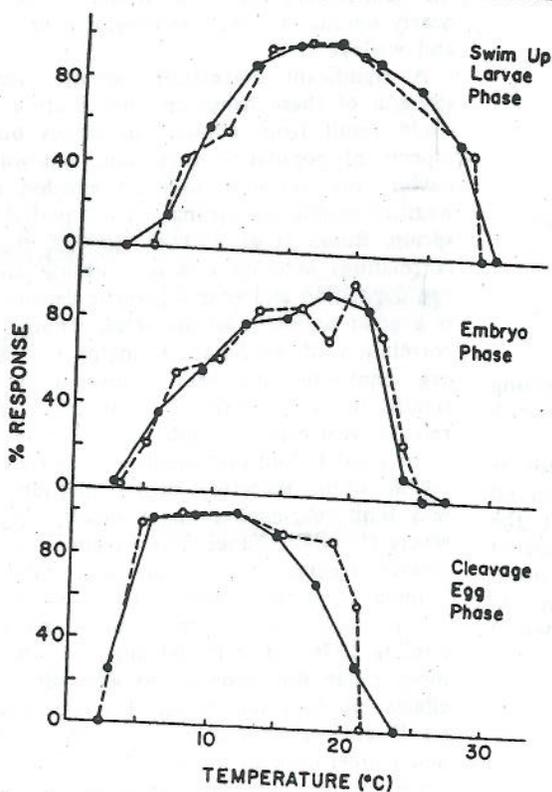


FIG. 2. Comparison of survival probabilities of early development phases of yellow perch predicted by model (●) and observed by Hokanson and Kleiner (1974) (○).

motivated this choice. First, year-class strength of walleye in the western basin of Lake Erie over the period of 1959-70 had a significant correlation to the temperature regime in the spring (Busch et al. 1975), and a similar relationship seemed to hold for perch (Hartman 1972). Second, daily temperatures of surface waters at South Bass Island were available for the period 1918-76 from the Ohio Department of Natural Resources (1961; and unpublished data). Third, the walleye and yellow perch populations in Lake Erie were highly exploited during this period. Under this condition we would expect recruitment to be most sensitive to climatic fluctuations. The application of this model for yellow perch and walleye assumed that the two species have the same physiological dependence on temperature. Although Hokanson (1977) suggested that walleye may be a few degrees less tolerant than yellow perch, Kitchell et al. (1977) were successful in describing temperature dependence of walleye growth using parameters derived for perch. Thus, given the similarity in their ranges and life history we considered that this assumption was not unreasonable.

Predicted survival of the early life-history stages of both yellow perch and walleye did not agree with the observed patterns of year-class strength in the western basin of Lake Erie. The joint-survival probability for 1959-70 had a relatively narrow range, 0.087 in 1967 to 0.132 in 1960 (Table 4), which contrasts with the 74-fold range for walleye and 18-fold range for yellow perch (Table 5). Using a nonparametric measure of rank correlation (Spearman r_s , Conover 1971), no significant correlation could be detected between predicted survival and observed year-class strength of either yellow perch or walleye, but

TABLE 4. Predicted survival probabilities of various life-history stages of yellow perch and the joint-survival probability (P) of the early life history from egg fertilization through age 0 juveniles, 1960-70. Life-history intervals reported are cleavage egg (P₁), embryo (P₂), swim-up larvae (P₃), pelagic larvae (P₄), and age-0 juvenile (P₅).

Year	P ₁	P ₂	P ₃	P ₄	P ₅	P
1960	0.971	0.695	0.895	0.997	0.366	0.132
1961	0.979	0.654	0.922	0.997	0.370	0.131
1962	0.972	0.640	0.911	0.996	0.347	0.118
1963	0.963	0.619	0.847	0.996	0.335	0.101
1964	0.954	0.639	0.924	0.996	0.334	0.112
1965	0.953	0.692	0.917	0.996	0.343	0.124
1966	0.903	0.614	0.815	0.999	0.350	0.095
1967	0.971	0.572	0.736	0.997	0.354	0.087
1968	0.974	0.715	0.906	0.997	0.341	0.129
1969	0.970	0.601	0.870	0.997	0.376	0.114
1970	0.972	0.660	0.901	0.997	0.331	0.114

TABLE 5. Rates of spring warming and indices of year-class strength in walleye and yellow perch of western Lake Erie, 1960-70.

Year	Rate of warming (°C/day) ^a	Walleye ^b	Perch ^c
1960	0.18	0.4	420
1961	0.24	7.8	1300
1962	0.29	29.6	2800
1963	0.20	1.5	210
1964	0.32	11.0	330
1965	0.36	11.1	2300
1966	0.10	0.6	160
1967	0.13	3.4	340
1968	0.12	1.7	160
1969	0.24	5.2	180
1970	0.31	28.2	640

^aMean daily rate of temperature increase from April to mid-May (Busch et al. 1975).

^bNumber of young-of-the-year walleye caught per hour of trawling (from Busch et al. 1975).

^cNumber of young-of-the-year perch caught per hour of trawling (from Leach and Nepszy 1976).

significant correlation between spring warming and both walleye year-class strength and yellow perch year-class strength.

Comparison of predicted survival of walleye YCS and yellow perch YCS vs. observed year-class strength of walleye YCS and yellow perch YCS. Rate of warming vs. walleye YCS and yellow perch YCS.

The correlation between walleye year-class strength and observed year-class strength was significant (Busch et al. 1975). Although the predicted survival of walleye year-class strength did not correlate with observed year-class strength, the timing of the hatch of walleye over a range of April to May was similar to the observed range of mid-May (Busch et al. 1975).

Year	r
1960	
1961	
1962	
1963	
1964	
1965	
1966	
1967	
1968	
1969	
1970	

Thus, the temperature regime seemed to be more important than survivorship.

Our simulation of temperature effects on life-history phases of walleye and yellow perch to determine the year-class strength in Lake Erie. Although the mortality of 90% of the mortal year-classes depends on the joint-survival probability of the early life-history phases, a significant correlation was found between predicted survival and observed year-class strength.

of the early life-history perch and walleye did not reveal patterns of year-class strength in western Lake Erie. The relative probability for 1959-70 had a relative probability of 0.087 in 1967 to 0.132 in 1968, a 1.5-fold contrast with the 74-fold range for yellow perch and the 18-fold range for walleye. A nonparametric measure of year-class strength (Conover 1971), which could be detected by a test of observed year-class strength for low perch or walleye, but

probabilities of various life-history stages for perch and the joint-survival probability life history from egg fertilization to juveniles, 1960-70. Life-history stages include average egg (P_1), embryo (P_2), pelagic larvae (P_3), and age-0

P_3	P_4	P_5	P
0.895	0.997	0.366	0.132
0.922	0.997	0.370	0.131
0.911	0.996	0.347	0.118
0.847	0.996	0.335	0.101
0.924	0.996	0.334	0.112
0.900	0.996	0.343	0.124
0.900	0.999	0.350	0.095
0.736	0.997	0.354	0.087
0.906	0.997	0.341	0.129
0.870	0.997	0.376	0.114
0.901	0.997	0.331	0.114

warming and indices of year-class strength for yellow perch of western Lake Erie

Walleye ^b	Perch ^c
0.4	420
7.8	1300
29.6	2800
1.5	210
11.0	330
11.1	2300
0.6	160
3.4	340
1.7	160
5.2	180
28.2	640

temperature increase from April to May

1960-70 year walleye caught per hour of observation (Nepson et al. 1975)

1960-70 year perch caught per hour of observation (Nepson et al. 1976)

significant correlations are found for rate of spring warming and both walleye and yellow perch year-class strength and for walleye year-class strength and yellow perch year-class strength:

Comparison	Correlation coefficient	
	r_s	P
Predicted survival vs. walleye YCS	0.091	>0.1
Predicted survival vs. yellow perch YCS	0.382	>0.1
Walleye YCS vs. yellow perch YCS	0.664	<0.025
Rate of warming vs. walleye YCS	0.841	<0.001
Rate of warming vs. yellow perch YCS	0.682	<0.025

The correlation between rate of spring warming and walleye year-class strength is consistent with the observations by Busch et al. (1975).

Although the predicted survival probabilities did not correlate significantly with observed walleye year-class strength, predictions of the timing of the hatch were much better. Predicted hatching of walleye (swim-up phase) occurred over a range of April 27-May 15, and the observed range of midhatching for the same period was May 1-12 (Busch et al. 1975):

Year	Observed date of midhatching	Predicted date of hatching
1960	May 10	May 8
1961	May 12	May 15
1962	May 4	May 4
1963	May 3	May 1
1964	May 7	May 9
1965	May 11	May 11
1966	May 8	May 4
1967	May 8	May 1
1968	May 1	April 27
1969	May 6	May 5
1970	May 11	May 5

Thus, the temperature dependence of development seemed to be more accurately described than survivorship.

Discussion

Our simulation results indicate that direct temperature effects on mortality of various early life-history phases of perch and walleye may not determine the year-class strength in western Lake Erie. Although the model accounts for about 90% of the mortality as due to temperature dependence of mortality, the narrow range of the joint-survival probability and the absence of any significant correlation of joint-survival probability to observed year-class strength argue against a

regulatory role for the temperature regime. In fact, the relatively high survival probabilities through the pelagic larvae phase may indicate that the temperature regime in western Lake Erie is nearly optimal for normal development of perch and walleye.

A significant correlation between year-class strength of these fishes and temperature regime could result from climatic influences on other aspects of population regulation. Spawning behavior, for example, may be affected by the weather conditions during a 2-wk period in the spring. Busch et al. (1975) reported significant correlations between rate of warming and both egg deposition and year 0 juvenile density, which is a good predictor of year-class strength. Rank correlation of year-class strengths indicated by egg deposition and year 0 juvenile density is significant ($r_s = 0.64$, $P < 0.025$). Thus the relative year-class strength in Lake Erie appears to be fixed before our simulations started.

Our results, therefore, suggest that temperature may limit year-class strength directly only under severe climatic regimes. These regimes occur with greatest frequency at the northern and southern boundaries of the ranges of these percid species, but may also occur periodically elsewhere (cf. Kipling 1976). The model might be used to explore range limitation or to determine possible effects of thermal stress. The occurrence of significant correlations between year-class strength and temperature in the middles of the ranges of these species, however, cannot be explained by the model we formulated. Spawning behavior, availability of specific types of food at various critical phases of development, predation and cannibalism rates, mortality of adults, and various abiotic factors may also have some correlation with temperature or act synergically with the physiological effects of temperature. Temperature effects on growth rate (e.g. Kitchell et al. 1977), for example, may prolong exposure to some other mortality factor.

Many of these interactions might be evaluated with the type of model developed here. For instance, joint effects of temperature and food density on growth and survival probabilities of larval percid could be incorporated by using some bio-energetic model (e.g. Brett et al. 1969; Kitchell et al. 1974; Kitchell et al. 1977). Inclusion of predation models that relate survival probabilities to development phase, temperature, alternative prey densities, and predator density (e.g. Menshutkin et al. 1968) might expand the use of this model to examine the role of predation and cannibalism in regulating year-class strength. Unfortunately, sufficient data to support these model extensions is rarely available for any

single percid population. Data requirements include stock size, age distribution, recruitment, seasonal temperature regime at location of fish stock, spawning time and temperature, periods of occurrence of various development phases, specific food biomass, and predator density. While it might be said that the existence of such data sets would obviate the need for a model, this approach or a similar one proposed by Kipling (1976) may nevertheless aid future experimental design in sorting out causal relationships.

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